# ATTRACTION OF *Ceratitis capitata* (DIPTERA: TEPHRITIDAE) FLIES TO ODOR OF COFFEE FRUIT

# RONALD J. PROKOPY1.\* and ROGER I. VARGAS2

<sup>1</sup>Department of Entomology University of Massachusetts Amherst, Massachusetts 01003 <sup>2</sup>USDA Tropical Fruit and Vegetable Research Laboratory Honolulu, Hawaii 96804

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Abstract-On potted nonfruiting host trees in outdoor field cages, we evaluated attraction of released mature laboratory-cultured or wild-origin Mediterranean fruit flies (medflies) to odor of freshly picked fruit of host and nonhost plants. Odor of ripe intact or crushed coffee fruit (the presumed ancestral host of medflies) was significantly more attractive than odor of ripe intact or crushed fruit of five lower-ranking hosts and three nonhosts. Odor of crushed coffee fruit was significantly more attractive than odor of intact coffee fruit. Odor of ripe or near-ripe coffee fruit was significantly more attractive than odor of unripe coffee fruit. Immature females (without eggs) were significantly more attracted to odor of a proteinaceous food lure than to odor of ripe coffee fruit, whereas the reverse was true for mature females carrying a high egg load. In some trials, males proved as discriminating as females in favor of coffee fruit odor, but in several other trials males were less discriminating than females. Response patterns of mature laboratorycultured females were similar to those of mature wild-origin females. In a field of coffee plants, attraction of natural-population females was significantly greater to odor of ripe coffee fruit than to water but was not greater than attraction to odor of proteinaceous food. Findings are discussed in relation to potential use of synthetic volatiles of coffee or other host fruit in traps for monitoring or controlling medflies.

Key Words-Attractants, odor, host fruit, coffee fruit, Ceratitis capitata.

<sup>\*</sup>To whom correspondence should be addressed.

#### INTRODUCTION

Numerous kinds of insects are known to be attracted to odor of their host plants. Most examples involve monophagous or oligophagous species, but in a few cases, polyphagous insects also have exhibited attraction to host plant odor (examples given in Bernays and Chapman, 1994). In tephritid flies, adult attraction to the odor of host fruit in favorable condition for oviposition has been demonstrated in the monophagous papaya fruit fly, *Toxotrypana curvicauda* Gerstaecker (Landolt et al., 1992), the monophagous olive fruit fly, *Bactrocera oleae* (Gmelin) (Scarpati et al., 1993), the oligophagous apple maggot fly, *Rhagoletis pomonella* (Walsh) (Prokopy et al., 1973; Averill et al., 1988), the polyphagous oriental fruit fly, *Bactrocera dorsalis* Hendel (Jang and Light, 1991), the polyphagous Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Eisemann and Rice, 1992), and the polyphagous Caribbean fruit fly, *Anastrepha suspensa* (Loew) (Nigg et al., 1994).

The Mediterranean fruit fly (medfly), Ceratitis capitata (Wiedemann), is a highly polyphagous tephritid that oviposits and develops in more than 300 species of fruits and vegetables (Liquido et al., 1991). To date most studies of medfly reaction to plant odor have involved measuring electroantennogram responses to a spectrum of plant volatiles, including several volatile constituents of host fruit and foliage (e.g., Guerin et al., 1983; Light et al., 1988, 1992). Regarding behavioral responses of medflies to plant odor, Levinson et al. (1990) presented laboratory-cage evidence suggesting lack of medfly attraction to odor of oranges, Citrus sinesis (a principal host), but in field cage tests, Katsovannos et al. (1995) have shown that both sexes of medflies are in fact attracted to odor of oranges. Using an outdoor olfactometer, Keiser et al. (1975) demonstrated significantly greater captures of medflies in traps baited with solvent extracts of various structures of a wide variety of plants (nearly all of which were nonhosts) compared with captures in unbaited traps. Finally, under field conditions, Guerin et al. (1983) found that medflies were attracted to traps baited with heptanal, a constituent of the fruit of several medfly host plants.

Here, in tests conducted in a patch of nonfruiting host trees in an outdoor field cage, we asked whether medflies were more attracted to odor of the fruit of coffee, Coffea arabica (the presumed ancestral host of medflies in Africa (Vargas et al., 1995)), than to odor of lower-ranking host fruit and nonhost fruit. We also asked whether both sexes were equal in discrimination among fruit odors of the various types tested, whether crushed fruit was more attractive than intact fruit, whether ripe fruit was more attractive than unripe fruit, whether attraction to host fruit odor was greater or lesser than that to food odor among flies of differing physiological states, and whether response patterns of wild-origin medflies differed from those of laboratory-cultured medflies. Finally, we

asked whether natural-population medflies in the field exhibited a level of response to host fruit odor similar to that of medflies in the field cage.

## METHODS AND MATERIALS

Medflies used in field cage tests originated either from a laboratory colony in culture for 10 generations at the USDA Tropical Fruit and Vegetable Research Laboratory in Honolulu or from natural-population larvae that infested field-collected coffee fruit. Unless indicated otherwise, from eclosion until tested 7–10 days afterward (for lab-cultured flies) or 14–18 days afterward (for wild-origin flies), both sexes were held together in 30-  $\times$  30-  $\times$  30-cm screened cages supplied with protein (enzymatic yeast hydrolysate), sucrose, and water but not fruit under laboratory conditions of about 25°C, 50% relative humidity, and 13 hr natural daylength.

Besides coffee, fruit used in field cage trials included five species that we considered to be low-ranking host fruit because in a 36-year survey in Hawaii (Liquido et al., 1990), only 1-9% of collected batches proved to be infested by medfly larvae (compared with 65% of collected coffee fruit batches found to be infested). These low-ranking host fruit included: guava, Psidium guajava; banana, Musca paradisiaca; tangerine, Citrus reticulata; papaya, Carica papaya; and avocado, Persea americana. We also evaluated three species of fruit that we considered to be nonhosts of medfly because none of the batches collected by Liquido et al. (1990) were found to be infested by medfly. These included: squash, Cucurbita maxima; macadamia nut, Macadamia integrifolia; and lipstick plant, Bixa orellana. All fruit were picked fresh from fruiting plants and placed immediately at 3°C until testing, which occurred 4-96 hr after picking. Unless stated otherwise, only fruit that we considered to be ripe and in optimum condition for potential medfly oviposition were picked and tested. Two hours before testing, fruit were rinsed with water, allowed to dry, and warmed to 25°C.

The first series of field cage experiments involved assessing attractiveness of odor of intact fruit of each type. In these and all other experiments, fruit of a single type was placed in a cylindrical clear-plastic container ( $11 \times 13$  cm) whose side and bottom was covered with aluminum foil to obscure visibility of fruit within. All but the 1-cm periphery of the clear-plastic lid consisted of nylon netting that effectively obscured visibility of fruit but permitted air flow. The number of fruit placed in each container was adjusted so that a total of  $\sim 140$  cm<sup>2</sup> of fruit surface area was exposed to air. With coffee, this was equivalent to 30 fruit that filled to capacity the floor of the container. In cases where the surface area of a single intact fruit exceeded  $\sim 140$  cm<sup>2</sup>, excess area was tightly

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enveloped in aluminum foil to prevent odor escape. The second series of field cage experiments involved assessing attractiveness of the odor of 5 g per container of freshly crushed skin and flesh of fruit of each type. Succeeding field cage experiments involved primarily the evaluation of medfly response to the odor of various conditions of coffee fruit or Nulure (Miller Chemical Co., Hanover, Pennsylvania), a proteinaceous food-type attractant. We formulated Nulure according to Wakabayashi and Cunningham (1991): 9% Nulure, 5% sodium borate, and 86% water. We used an amount that covered the floor of the container.

All field-cage trials were carried out from 09:00–16:00 hr in a cylindrical, 3-m-tall  $\times$  3-m-diam., clear nylon-screen enclosure placed outdoors on the grounds of the USDA Tropical Fruit and Vegetable Research Laboratory in Honolulu. The top of the enclosure was covered with a partly opaque tarpaulin to exclude direct sunlight and rainfall. Flow of wind through the cage was regulated to 0–3 km/hr by using an adjustable, clear-plastic wind barrier at the upwind side of the cage wall. The cage contained four potted nonfruiting guava trees grouped near the center of the cage to form a continuous canopy (120 cm tall  $\times$  220 cm diam.). Before use, the foliage and stems of each tree were rinsed thoroughly with water.

At each of four positions within the canopy, we hung a single container of test substance. The positions were about 90 cm apart along the circumference of an imaginary circle about 20 cm inward from the periphery of the upper part of the canopy. For each replicate of each experiment, about 25 flies of each sex were released as a group at the lower center of the canopy. We assumed (but did not document) a 50:50 sex ratio of released flies. Flies that arrived on the screened area of the lid of a container within the 5-min period allotted each replicate were considered as responding to odor of the contents, were sexed, and were removed by an aspirator. Treatment positions were randomized for the first replicate. Treatments were rotated clockwise within the canopy after each replicate until each treatment occupied each position once, requiring a total of about 25 min to complete a set of four replicates. For the next set of four replicates, we used a fresh batch of fruit. Most nonresponding flies had flown to the cage wall by the end of a replicate. To shorten time and hence minimize changes in the state of fruit over the course of testing, we adopted a 5-min test period rather than a longer test period and we did not collect and remove nonresponding flies until the end of an experiment. A separate batch of flies was used for each experiment. During experiments, temperature within the tree canopy ranged from 24 to 31°C.

The field test was conducted in a plantation of coffee plants on Kauai (Vargas et al., 1995) which, at the time of testing in March 1995, had recently been harvested. Very few fruit remained. A container of test substance was

inserted into a hole in the center of a 25-  $\times$  25-cm piece of horizontal brown cardboard in such a way that the screened lid of the container protruded about 3 cm above the Tangletrap-coated upper surface of the cardboard. Such traps were suspended 10 m apart from the branches of coffee plants. After 1 hr, captured natural-population medflies were counted and removed, the test fruit was replaced with freshly prepared batches, and the containers were moved to new positions.

Data were analyzed by two-way analysis of variance (ANOVA). Treatment means were compared using the least significant difference test criterion (0.05 level). For ANOVA, the 16 replicates per treatment per experiment were grouped into four sets of four replicates each. For each treatment, the value of a single set of four replicates consisted of the number of flies arriving on the screen of a container for all four positions of that treatment combined. We reasoned that grouping the data into sets of replicates for ANOVA was the most valid approach to minimizing varying effects of treatment position within the tree canopy on fly response to replicates within a set.

## RESULTS

Field Cage Tests. In four experiments involving intact fruits, the odor of ripe coffee fruit was significantly more attractive to mature (egg-bearing) laboratory-cultured females than was the odor of five kinds of ripe low-ranking host fruit (guava, tangerine, papaya, banana, and avocado) or the odor of three kinds of ripe nonhost fruit (squash, macadamia nut, and lipstick plant) (Table 1). Except for papaya and avocado, the odor of low-ranking hosts was more attractive than water. Except for macadamia nut, the odor of nonhosts was not more attractive than water. In these four experiments, significantly more males were attracted to coffee odor than to the odor of tangerine, papaya, banana, or avocado (but not guava) (Table 1). Among low-ranking hosts, only the odor of banana attracted significantly more males than water. Except for lipstick plant, the odor of nonhosts was no more attractive to males than was water.

In four similarly designed experiments that involved comparing the response of mature laboratory-cultured medflies to the odor of crushed ripe fruit, again significantly more females were attracted to coffee odor than to the odor of any low-ranking host fruit or nonhost fruit (Table 1). Again, except for papaya and avocado, the odor of low-ranking hosts was more attractive than water, and, except for macadamia nut, the odor of nonhosts was no more attractive than water. In these four experiments, significantly more males were attracted to coffee odor than to the odor of papaya and avocado (but not guava, banana, or tangerine) (Table 1). Among low-ranking hosts, the odor of banana and tangerine (but not papaya, guava and avocado) attracted significantly more males

TABLE 1. ATTRACTION OF MATURE RELEASED LABORATORY-CULTURED C. capitata
FLIES TO ODOR OF INTACT OR CRUSHED RIPE HOST OR NONHOST FRUIT IN CONTAINERS
IN NONFRUITING FIELD-CAGED TREES

|            |                 |            | Arriving flies (mean N) per replicate" |       |
|------------|-----------------|------------|--|-------|
| Experiment | Fruit condition | Fruit type | Females                                | Males |
| 1          | Intact          | Coffee     | 5.7a                                   | l.la  |
|            |                 | Guava      | 2.6b                                   | 0.6ab |
|            |                 | Squash     | 1.9bc                                  | 0.6ab |
|            |                 | Water      | 1.3c                                   | 0.1b  |
| 2          | Intact          | Coffee     | 6.9a                                   | 1.3a  |
|            |                 | Tangerine  | 2.0b                                   | 0.4b  |
|            |                 | Papaya     | 1.6bc                                  | 0.3b  |
|            |                 | Water      | 0.3c                                   | 0.4b  |
| 3          | Intact          | Coffee     | 8.3a                                   | 3.6a  |
|            |                 | Banana     | 4.3b                                   | 1.6b  |
|            |                 | Mac Nut    | 1.9c                                   | 1.1bc |
|            |                 | Water      | 0.3d                                   | 0.5c  |
| 4          | Intact          | Coffee     | 8.6a                                   | 3.3a  |
|            |                 | Avocado    | 1.9b                                   | 0.6bc |
|            |                 | Lipstick   | 2.6b                                   | 2.3ab |
|            |                 | Water      | 1.8b                                   | 1.1c  |
| 5          | Crushed         | Coffee     | 5.9a                                   | 3.3a  |
|            |                 | Guava      | 3.3b                                   | 2.0ab |
|            |                 | Squash     | 1.4c                                   | 1.3ab |
|            |                 | Water      | 1.1c                                   | 0.8b  |
| 6          | Crushed         | Coffee     | 6.3a                                   | 3.1a  |
|            |                 | Tangerine  | 3.3b                                   | 2.8a  |
|            |                 | Papaya     | 1.9bc                                  | 1.1b  |
|            |                 | Water      | 0.4c                                   | 0.6b  |
| 7          | Crushed         | Coffee     | 10.2a                                  | 4.8a  |
|            |                 | Banana     | 5.0b                                   | 4.4a  |
|            |                 | Mac Nut    | 4.4b                                   | 2.1b  |
|            |                 | Water      | 1.4c                                   | 1.1b  |
| 8          | Crushed         | Coffee     | 9.0a                                   | 2.1a  |
|            |                 | Avocado    | 1.4b                                   | 0.5b  |
|            |                 | Lipstick   | 2.0b                                   | 2.5a  |
|            |                 | Water      | 0.9b                                   | 0.6b  |

<sup>&</sup>quot;Sixteen replicates per treatment. Values in each column in each experiment followed by the same letter are not significantly different at the 0.05 level according to least significant difference tests.

than water. Except for lipstick plant, the odor of nonhosts was no more attractive to males than water.

Each sex of mature laboratory-cultured medflies was significantly more attracted to the odor of 30 ripe crushed coffee fruit than to the odor of 30 ripe intact coffee fruit (Table 2). The odor of 30 ripe (dark red) and 30 near-ripe (orange-red) intact coffee fruit was no different in attractiveness to either sex of laboratory-cultured medfly; each was significantly more attractive to each sex than the odor of 30 unripe (green) intact coffee fruit, which proved to be no more attractive than water (Table 2).

One-day-old, laboratory-cultured, protein-fed females were significantly more attracted to the odor of Nulure than to the odor of 30 intact ripe coffee fruit, which was no more attractive than water or an empty container (Table 3). Three-day-old, laboratory-cultured, protein-fed females (having immature eggs only) responded similarly to 1-day-old females, except that coffee odor was now significantly more attractive than water or an empty container. In contrast, 10-day-old, laboratory-cultured, protein-fed females (having a large complement of mature eggs) were significantly more attracted to coffee odor than to Nulure, which was no more attractive than water or an empty container. Ten-day-old, laboratory-cultured, protein-deprived females (that had received only sucrose since eclosion) responded similarly to 3-day-old protein-fed females. The response pattern of 1-day-old and 10-day-old protein-fed males was the same as that of equivalent-type females, but 3-day-old protein-fed males and 10-day-old protein-deprived males did not discriminate among treatments (Table 3).

Table 2. Attraction of Mature Released Laboratory-Cultured *C. capitata*Flies to Odor of Intact or Crushed Ripe Coffee Fruit and Odor of Coffee
Fruit in Three Stages of Ripeness in Containers in Nonfruiting Field-Caged
Trees

|            |                 | _       | Arriving flies (mean N) per replicate" |  |
|------------|-----------------|---------|--|--|
| Experiment | Fruit condition | Females | Males                                  |  |
| 1          | Intact          | 1.8b    | 1.6b                                   |  |
|            | Crushed         | 4.6a    | 4.4a                                   |  |
| 2          | Green           | 3.5b    | 1.7b                                   |  |
|            | Orange-red      | 9.0a    | 4.1a                                   |  |
|            | Dark red        | 10.9a   | 5.3a                                   |  |
|            | Water           | 1.5b    | 0.6b                                   |  |

<sup>&</sup>quot;See footnote of Table 1.

Table 3. Attraction of Released Laboratory-Cultured *C. capitata* Flies of Different Ages or Protein-Access Treatments to Odor of Intact Ripe Coffee Fruit or Proteinaceous Food (Nulure) in Containers in Non-Fruiting Field-Caged Trees

|            | Condition of flies        | Type of attractant | Arriving flies (mean N) per replicate" |       |
|------------|---------------------------|--------------------|--|-------|
| Experiment |                           |                    | Females                                | Males |
| 1          | One day old,              | Coffee             | 0.8b                                   | 0.4b  |
|            | protein fed               | Nulure             | 2.8a                                   | 1.4a  |
|            | •                         | Water              | 0.3b                                   | 0.2b  |
|            |                           | None               | 0.1b                                   | 0.0b  |
| 2          | Three days old,           | Coffee             | 1.3b                                   | 0.4a  |
|            | protein fed               | Nulure             | 3.0a                                   | 0.3a  |
|            | •                         | Water              | 0.4c                                   | 0.1a  |
|            |                           | None               | 0.4c                                   | 0.0a  |
| 3          | Ten days old,             | Coffee             | 2.8a                                   | 1.6a  |
|            | protein fed               | Nulure             | 0.6b                                   | 0.4b  |
|            | •                         | Water              | 0.6b                                   | 0.6b  |
|            |                           | None               | 0.6b                                   | 0.5b  |
| 4          | Ten days old, Coffee 2.1b | 2.1b               | 0.0a                                   |       |
|            | protein deprived          | Nulure             | 3.1a                                   | 0.5a  |
|            | •                         | Water              | 0.3c                                   | 0.1a  |
|            |                           | None               | 0.1c                                   | 0. la |

<sup>&</sup>quot;See footnote of Table 1.

Table 4. Attraction of Mature Released Laboratory-Cultured or Wild  $\it C.$   $\it capitata$  Flies to Odor of Intact Ripe Coffee or Guava Fruit or Proteinaceous Food (Nulure) in Containers in Nonfruiting Field-Caged Trees

| Experiment |               | T f                | Arriving flies (mean N) per replicate" |       |
|------------|---------------|--------------------|--|-------|
|            | Type of flies | Type of attractant | Females                                | Males |
| 1          | Lab-cultured  | Coffee             | 2.4a                                   | 3.2a  |
|            |               | Guava              | 0.9b                                   | 1.1b  |
|            |               | Nulure             | 0.6b                                   | 1.1b  |
|            |               | Water              | 0.6b                                   | 0.6b  |
| 2          | Wild          | Coffee             | 2.6a                                   | 0.3a  |
|            |               | Guava              | 1.1b                                   | 0.3a  |
|            |               | Nulure             | 1.3b                                   | 0.8a  |
|            |               | Water              | 0.4b                                   | 0.1a  |

<sup>&</sup>quot;See footnote of Table 1.

Table 5. Attraction of Natural-Population *C. capitata* Flies to Odor of Crushed Ripe Coffee Fruit or Proteinaceous Food (Nulure) in Containers in a Field of Nonfruiting Coffee Plants

|                    | Arriving flie |       |
|--------------------|---------------|-------|
| Type of attractant | Females       | Males |
| Coffee             | 1.6a          | 0.2b  |
| Nulure             | 2.3a          | 2.7a  |
| Water              | 0.2b          | 0.6b  |

<sup>&</sup>quot;Same as footnote of Table 1 except 12 replicates per treatment.

When compared for attraction to the odor of equivalent surface areas of intact coffee fruit, intact guava fruit, Nulure, and water, mature, protein-fed, wild-origin and laboratory-cultured females responded similarly: they showed significantly greater attraction to coffee odor than to the odor of the other three treatments, among which there were no significant differences (Table 4). The same pattern held true for laboratory-cultured males but not for wild-origin males, which did not discriminate among treatment types (Table 4).

Field Test. Natural-population females in a coffee plantation were significantly more attracted to the odor of Nulure and 30 near-ripe crushed coffee fruit (no significant difference between these) than water (Table 5). Natural-population males were significantly more attracted to the odor of Nulure than to the odor of coffee fruit, which was no more attractive than water (Table 5).

## DISCUSSION

Our findings show that mature laboratory-cultured medfly females were attracted to the odor of near-ripe and ripe coffee fruit (particularly recently crushed fruit), but not to the odor of unripe coffee fruit. Female response was weaker to the odor of tested types of lower-ranking host fruit and generally lacking to the odor of tested types of nonhost fruit, irrespective of whether such fruit were intact or crushed. Laboratory-cultured females carrying no mature eggs proved to be more attracted to the odor of proteinaceous food (Nulure) than to the odor of ripe intact coffee fruit, but the reverse was true for mature, egg-bearing females. When directly compared, response patterns of mature wild-origin females proved similar to those of mature laboratory-cultured females. Natural-population females were found to be attracted to odor of both Nulure and coffee fruit.

This is the first published study to show that the odor of fresh-picked coffee

fruit, the presumed ancestral host of medflies, is more attractive to medflies than fruit odor of lower ranking host and nonhost plants. To our knowledge, there exist three other studies that have examined the potential attractiveness of coffee plant odor to medflies. First, Keiser et al. (1975) found significant attraction of medfly females and males to ether extracts of coffee bark and stems, but they did not make extracts of coffee fruit. Such extracts proved more attractive than extracts of foliage, bark, or stems of most nonhosts tested, but odor of some nonhosts (e.g., Diospyros discolor, Kallstroemia maxima) proved more attractive than coffee odor. Second, Vargas and Chang (1991) found that harvest of eggs from oviposition bottles that contained a hot water extract of canned coffee grounds was significantly greater than that from bottles that contained orange, guava, or papaya juice. Third, Lance, Jang, and McInnis (unpublished data) have recent evidence that somewhat parallels the findings of our study: crushed ripe coffee fruit is attractive to both sexes of medflies under laboratory windtunnel as well as field conditions. Further research is needed to determine whether the odor of coffee fruit is more or less attractive than the odor of coffee foliage, stems, or woody tissue.

Our finding that the odor of near-ripe and ripe coffee fruit is much more attractive to medflies than the odor of unripe coffee fruit is consistent with the finding of Vargas et al. (1995) that oviposition by natural-population medflies in commercial plantations was dramatically (30 to 70-fold) greater in ripe than unripe coffee fruit. Similarly, Carle et al. (1987) showed that the odor of host fruit of *R. pomonella* was much more attractive to the flies when fruit was ripe than unripe. Furthermore, Jang and Light (1991) found that odor of host fruit of *B. dorsalis* increased in attractiveness to the flies with increasing ripeness of fruit. Together, these findings suggest that future study of the identity of volatile components of coffee plants attractive to medflies should be focused on plants whose fruit are near-ripe or ripe.

We were not surprised that the odor of freshly crushed coffee fruit was more attractive to medflies than the odor of intact coffee fruit. First, one would expect that a greater amount of volatile chemicals is released from recently wounded plant tissue than intact plant tissue (Finch, 1980). Second, Papaj et al. (1989, 1992) demonstrated that medfly females in search of egg-laying sites can respond positively and quickly to recent natural or artificial punctures in host fruit. Exploitation of fresh punctures as potential oviposition sites may be adaptive when females are limited in time available to drill punctures in fruit or when fruit are resistant to puncturing (Papaj et al., 1992), particularly in habitats where predators of ovipositing females are abundant (Papaj et al., 1989). Selection may have given rise to a high level of medfly sensitivity to the odor of host fruit released from fresh punctures (magnified here in the form of freshly crushed host fruit).

Our finding that female medflies were in several instances more responsive to coffee fruit odor than were male medflies parallels the finding of Keiser et al. (1975) that females were somewhat more attracted than males to the odor of coffee stems and bark. In addition, both Levinson et al. (1990) and Light et al. (1992) describe several instances of greater antennal receptor sensitivity of female than male medflies to host fruit volatiles. The biological basis of more frequently detected positive responses of medfly females than males to host odor is uncertain, but it could reside in a strong influence upon females of host odor as indicative of host plants or individual host fruit that are potentially favorable egg-laying sites, whereas host odor might have only a weak influence upon males as indicative of potentially favorable mating sites. Mating in medflies apparently occurs in the vicinity of host plants but is not always restricted to host plants (Hendrichs and Hendrichs, 1990).

The physiological state of an insect and the structure of the resource environment may have important effects on the order in which an insect prioritizes its visits to essential types of resources, such as feeding and egg-laying sites. Precisely how hunger and egg load interact in shaping resource foraging behavior has received considerable attention in insects such as Blatella cockroaches. Phormia and Lucilia blowflies, Musca face flies, Glossina tsetse flies, and several species of mosqitoes that have distinct ovarian cycles in which response to food stimuli and feeding gradually decline as a developing batch of oocytes approaches maturity (reviewed in Barton Browne, 1993). In tephritid flies, there is strong evidence indicating that B. tryoni and R. pomonella females denied access to protein and lacking fully developed eggs are more attracted to proteinaceous food than to egg-laying sites, whereas the opposite is true for females provided with protein and carrying moderate to large egg loads (Prokopy et al., 1991, 1995). Our findings here with laboratory-caged medflies whose age and diet prior to testing in field cages were carefully defined are consistent with the pattern exhibited by B. tryoni and R. pomonella. Unfortunately, we had no knowledge of fly age or feeding history in our study of natural-population medflies in the coffee field. We can only speculate that for whatever reason, those captured were roughly equally divided between females seeking proteinaceous food and females seeking egg-laying sites.

Together, the results of this study have implications for the design of traps used to monitor or control medflies. For example, current traps for medfly females rely solely upon proteinaceous food-type stimuli such as Nulure as attractants (Millar, 1995). If the environment in which food-type traps are placed has abundant natural food, such as honeydew or bird droppings (Nishida, 1980; Prokopy et al., 1992), or if females are not hungry for protein, then food-type traps may be comparatively ineffective in luring medflies. Synthetic host fruit odor could be a valuable complement to food odor in that it could attract females

seeking oviposition sites rather than food. Traps baited with synthetic fruit odor alone have proven very effective in monitoring R. pomonella flies in apple orchards (Agnello et al., 1990), while traps baited with a combination of synthetic food and synthetic fruit odor have provided good to excellent commercial control of R. pomonella (Prokopy et al., 1994). As pointed out by Millar (1995), competition from fruit odor emitted by host plants themselves and prior experience of natural-population females would have to be considered when developing strategies for deploying medfly traps baited with synthetic fruit odor. Before an intensive effort is made to identify and synthesize host volatiles attractive to female medflies, however, further study is needed to pinpoint which coffee plant structures and which phenological stages of coffee plant development do in fact emit the most attractive odor. Moreover, further study is needed to determine if the odor of coffee plants is more attractive than the odor of other high-ranking host plants of medfly. Finally, research is needed to assess whether a combination of host fruit odor and proteinaceous food odor is more attractive to natural-population medflies than either type of odor alone.

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